also belongs to a group of larvae with distinctive scuta, while *E. perameles* is not placed even in a tentative subgenus (Audy, 1953). Further discussion of the true relationships of this nymph is impossible until other species have been reared and correlated with their larvae.

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NITROGEN ECONOMY IN SEMI-ARID PLANT COMMUNITIES.

PART I. THE ENVIRONMENT AND GENERAL CONSIDERATIONS.

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Synopsis.

An introduction to the nitrogen economy of semi-arid plant communities is presented. The significance of soil nitrogen and the decline in fertility are discussed with regard to the pastoral-erosion problem. Particular attention has been paid to the mulga (*Acacia aneura*) scrub in which premature death of timber is rife. Two soils from near-virgin mallee (Eucalypt-dominated) were included for comparison.

The investigations have shown that soil organic matter is highest in the mallee; so also is soil nitrogen. In the mulga scrub the soils of the stony ridges are higher in organic matter and nitrogen than those developed on the stable dunes. Erosion is responsible for the removal of organic matter and nitrogen, since low values of both organic matter and nitrogen occur in eroded soils, scalds, and sand dunes. Most of the organic matter and nitrogen occur in the surface three inches of soil. Nitrate levels are highest in the mallee, nitrate concentration being proportional to organic content.

The C/N ratio is highest in the least eroded soils. The drop in C/N ratio with increasing erosion may be due to the loss of CO_2 following oxidation of organic matter.

Soil nitrogen limits growth in all soils when water is adequate. Phosphate levels are relatively low, though they are never limiting; the phosphate is distributed fairly evenly down the profile.

Water-soluble salts are low. In the mallee the soil solution is dominated by Ca ions, in the mulga scrub by Na ions.

INTRODUCTION.

So little work has been done on the nitrogen economy of plant communities in general, and of semi-arid communities in particular, that no satisfactory conclusions concerning the sources of fixed nitrogen to a plant community can be made. This lack of information can be ascribed partly to the concentration of work on the isolation and intensive study of a single group of organisms concerned with nitrogen-fixation, and partly to the fact that the presence of nitrogen-fixing organisms in the community suggests that these organisms are supplying the community with all the fixed nitrogen contained within the soil-plant system. Thus when legumes dominate the community or occur in abundance, it is assumed that the legumes support the community as far as fixed nitrogen is concerned; on the contrary, when legumes are rare or absent, non-symbiotic organisms are assumed to supply the nitrogen. Nitrogen fixed in other ways, for example during thunderstorms, is usually regarded as of subsidiary importance, except in special cases, such as the high rainfall areas of the tropics. Likewise, those photosynthetic organisms now known to be nitrogen-fixers have been regarded as significant contributors to the nitrogen capital of a community only in special cases, as discussed in Russell (1950).

With regard to legume-fixation, it is relevant to mention here the following two very important observations. Firstly, many legumes do not normally nodulate (Allen and Allen, 1947). Secondly, some introduced legumes in Australia produce only ineffective nodules, or do not nodulate at all because of the absence of suitable *Rhizobia* or because of unsuitable soil conditions (Vincent, 1954).

Research in western New South Wales was commenced by the writers as a result of the widespread death of the mulga, *Acacia aneura*, which formerly dominated some thousands of square miles of semi-arid country in the central portion of Australia.

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The causes of death are unknown, nor are they relevant to the present discussion. The pertinent questions at the moment are whether the mulga is contributing to the nitrogen capital of the community and, if so, what effects the widespread death of the mulga is having on the nitrogen levels in the soil.

No detailed work on nitrogen fixation has hitherto been done in this area. The only quantitative data published are figures for total nitrogen and organic carbon quoted in bulletins dealing with soil surveys for land use and irrigation projects. Since no indication of the extent of erosion or the exact nature of the herbaceous vegetation is included, these data are of little value to the present investigations. The classical work of Jensen (1940) may well be mentioned here, since this author provides reliable bacteriological data for an area adjacent to, but wetter than, the area discussed in this paper. Jensen, working on soils from the wheat belt, has shown that non-symbiotic organisms operate significantly only over limited areas, and that the actual contribution of the nitrogen-fixers to the nitrogen capital of the soil is low as far as wheat growing is concerned.

In this present series of papers an attempt will be made to account for the various sources of nitrogen to a plant community, to evaluate quantitatively the effectiveness of the various contributors, to define the significance of the death of the mulga, and to evaluate the significance (if any) of mineral nutrition in pasture degeneration and in secondary successions. This first paper deals chiefly with the general features of the environment, which are particularly relevant to the nitrogen-fixing organisms. The occurrence and activity of these will be dealt with in succeeding papers.

The Plant Communities.

Of the five common plant communities that occur in the western portion of the State, only two have been studied. Of these, the mulga scrub, *Acacia aneura* Alliance (and its degenerate and successional communities) have received by far the most attention. A few observations have been made on the mallee (*Eucalyptus oleosa–E. dumosa* Alliance) for comparative purposes. These communities have been described in detail by Beadle (1948*a*).

The mulga scrub occurs chiefly in the north-western corner of the State, and by far the greater part of it lies within the 10-inch isohyet. It is restricted to soils of light texture, on rocky ridges or on stable sand dunes. On the ridges the soils are skeletal and are derived chiefly from schists, slates, quartzites, pegmatites and sandstones. They are shallow, rarely exceeding a foot in depth, and contain abundant unweathered minerals. The deep root systems of the mulga cannot be accommodated in the soils, but the roots penetrate clefts between rocks, especially when these are tilted, as is often the case. On the stable dunes the soils are derived from calcareous or non-calcareous sands which extend to depths of up to 20 feet or more. In spite of the marked differences in soil depth and in lime content, the structure and floristic composition of the communities in the two habitats is very similar. *Acacia aneura* is dominant (local dominants of non-leguminous plants sometimes occur); other shrub species of *Acacia* and of *Cassia* are common, while annual forbs are likewise abundant.

In contrast to the mulga scrub, the mallee, which occurs in a similar climate in the south-west corner of the State on sandy soils which are usually calcareous, is dominated by non-legumes (Eucalypts); both shrub-legumes and herbaceous legumes are rare or absent.

Following the destruction of the dominant shrubs or mallees either as a result of clearing or of premature death of the mulga, the herbaceous sward increases slightly in density, but this increase is short-lived when the country is stocked. Heavy grazing has led to the degeneration of the pasture and to soil erosion. The degenerate communities (which in most cases are secondary successional stages) are usually quite different floristically from the herbaceous stratum of the original community (Beadle, 1948*a*). In extreme cases, hard scalds, pseudo-scalds (Beadle, 1948*b*) or sand dunes result. These degenerate areas are of particular significance and will be referred to in more detail below.

Climate.

Most of the area under discussion experiences a steppe climate (Köppen's classification, as modified by Lawrence, 1937); a desert climate exists in the north-west corner of the State. The salient features of the climate are summarized as follows.

The mean annual rainfall for the area is 8 to 10 inches. It is not distributed regularly or seasonally, and single falls of rain rarely exceed 2 inches. Evaporation is of the order of 60 to over 100 inches per annum; consequently the soil surface is air-dried for much of the year. Maximum shade temperatures frequently exceed 40°C. for weeks on end during the summer; temperatures below freezing are infrequent during the winter. Winds of relatively high velocity occur at any time of the year, and during the summer, when the ground is bare, they produce dust storms which remove surface soil over long distances, or sandstorms which gradually lead to the development of scalds and sand dunes.

Soil temperatures under vegetation follow closely shade air temperatures; temperatures over 40°C. are rare. Temperatures on bare soil exceed air temperatures by up to 20° C. Measurements made in bare sandy country in the Broken Hill district between 2 and 3 p.m. on a hot cloudless day in December, with the air temperature at 43°C., indicate the following approximate summer soil temperatures:

0– 5 mm.	58°C.
10–20 mm.	44°C.
At 10 cm.	38°C.
Below dark-coloured litter	58°C.
In shade of living bushes	43°C.

It is interesting that the presence of loose litter on the soil surface has little effect on reducing the temperature, which is in contrast to the effect of shade thrown by living bushes onto the soil. These figures are significant with reference to the survival of micro-organisms, and will be referred to again.

Light intensity, relevant to photosynthetic organisms, has not been studied quantitatively. Qualitative observations indicate, however, that it is only in the mallee where the soil surface is sometimes strewn with a deep layer of litter that light intensity on the soil surface may be a limiting factor for the growth of photosynthetic organisms.

Quantitative Data on Relevant Soil Properties.

The data that are included in this section have been collected in order to elucidate the nutritional status of the original soils and their truncated profiles with regard to autotrophic plants and nitrogen-fixing organisms (bacteria and certain algae). Except for the few profiles that have been studied (all from the mulga scrub) the procedure has been to sample only the top three inches of soil, irrespective of the degree of truncation of the profile. When sampling, notes on the degree of erosion and the condition of the timber have been made so that correlations between erosion or timber death and the various soil properties can be made. The techniques used are given in the appendix.

Organic Carbon.

Quantitative data for surface samples are included in Table 1. In soils where erosion is apparently not significant, the highest organic content is found in the mallee. For the mulga scrub the soils on the ranges are significantly higher in organic matter than those on the dunes. This may be due to the concentration of organic matter on the ranges into pockets among the rocks, which are commonly exposed at the surface.

Erosion in all cases causes a marked decrease in the organic content of the soil. On the ranges, where water erosion predominates, the organic matter is removed with mineral soil and possibly accumulates at lower levels. However, on the dunes, where wind erosion is the predominant or sole agent of removal, the organic matter is winnowed out of the soil during dust storms, reducing the organic matter level to very low values. Furthermore, deflated drifting sand may be blown onto other soils, thus burying the organic matter of the latter and producing pseudo-profiles, as discussed in the next section.

Distribution of Organic Matter in the Soil Profile.

Samples were collected in selected sites to determine the distribution of organic matter in the soil profile. Unfortunately, the proximity of rock to the surface in the stony ridges precludes sampling beyond a depth of about nine inches. On the stable dunes, however, sampling was continued to a depth of about two feet in three sites where the soil was not apparently eroded, though in these areas deflation with loss of organic matter could have occurred. In contrast to these three sites a pseudo-profile consisting of a surface deposit of six inches of drift sand overlying a truncated or deflated profile was investigated, as well as three scalded areas. The results are given in Table 2.

The figures illustrate the following points. In apparently non-eroded soils the organic matter is most abundant at the surface. However, the sub-surface layers also contain, in comparison with the surface, a relatively high percentage of organic matter. This probably originates from the decomposition of roots in the soil. It is of particular interest that in the sub-surface layers the percentage of organic carbon is, in all cases, about 0·2%, a point which will be referred to below.

The pseudo-profile with its accumulated surface deposit represents a very widespread condition in the west. Although soils such as these appear to be non-eroded they are virtually some of the poorest in the mulga country, since they contain the extremely low levels of organic matter typical of the dunes whence the sand has blown. It is significant that in this profile the sub-surface layers contain some 0·2% organic carbon, the figure typical of the sub-surface on non-eroded soils.

In the case of scalds the organic carbon is low throughout; the sub-surface value of about 0·2% is repeated again. The surface layers of scalds, as the figures indicate, vary considerably. The lowest value recorded is 0·08% O.C. (hard scald), the highest 0·42% (soft scald). The latter high figure is possibly accounted for by the presence of surface films of organic matter accumulated by surface wash, from dead angiospermic colonizers, or from algal growths. The low value on the other hand may be the result not of winnowing, as in the case of dunes, but rather of the respiration of micro-organisms or by oxidation of the organic matter at high temperatures. The latter has been shown to be significant in certain soils by Dehérain and Demoussy (quoted in Demelon, 1944) and by Bunt and Rovira (1954).

Soil Nitrogen.

Quantitative data for soil nitrogen are given in Table 1. Figures for total nitrogen are low in all communities, except the mallee, where the mean value of 0·3% can be regarded as high for a semi-arid soil. Since the fixed nitrogen in these soils is contained within the organic matter, it follows that with increased erosion there is a progressive fall in total nitrogen.

Available Nitrogen.—Nitrate and ammonium were estimated chemically (Table 1). In all cases ammonium is very low. Nitrate, on the other hand, in some cases is relatively high. The highest figures were obtained from the soils from the mallee, where 19·4 and 29·4 p.p.m. N (76 to $>$100 p.p.m. NO_3) are comparable with nitrate levels in the average wheat soil. It is of interest that some of the mallee soils in this area have been sown to wheat, and satisfactory crops have been obtained when the rainfall was adequate. The amount of nitrate is closely correlated with the organic content, from which it may be concluded that (as would be expected) the nitrate is produced in the soil through the nitrification of ammonified organic N.

Available nitrogen was also estimated in pot culture, using oats as a test plant. The figures (Table 1) correspond well with chemical data and they indicate, in addition, that for all soils investigated available nitrogen is the limiting factor when moisture conditions are adequate, except in one mallee soil. Furthermore, the amount of growth of the oats in all except the non-eroded soils is low, so low in many cases, particularly for the scalds and sand dunes, that we may well suspect that soil nitrogen rather than soil moisture may be the factor determining the rate of the secondary succession under natural conditions. Further elaboration of this point is included in the discussion.